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THE CAMBIUM AND ITS DERIVATIVE TISSUES

III. A RECONNAISSANCE OF CYTOLOGICAL PHENOMENA IN THE CAMBIUM

I. W. Bailey

Introduction

In the second paper of this series, the writer (1920*b*) called attention to the fact that the dimensions and volume of the undifferentiated, actively dividing and growing cells of the lateral meristem or cambium vary greatly, not only in plants of different systematic affinities, but in different parts of a given individual and in stems grown under different environmental conditions. Therefore, the cambium provides an unusually favorable medium for the study of a number of fundamental cytological problems, particularly those of the "working sphere of the nucleus," the much discussed "nucleo-cytoplasmic relation," and phenomena of karyokinesis and cytokinesis in cells of unusual shapes and sizes.

Sachs (1893) held that, although plants vary enormously in their linear dimensions, their constituent cells are minute and of relatively uniform size. His student Amelung (1893) endeavored to prove, by means of an extensive series of measurements, that variations in the size of an organ or plant are due to differences in cell number rather than to fluctuations in cell size; a view which subsequently was championed on the zoological side by Conklin (1896, 1898), Rabl (1899), Driesch (1898, 1900), Schultz (1904), and others. Sachs (1892, 1893, 1895) and Strasburger (1893) concluded that the size of uninucleated cells, particularly of the undifferentiated cells of embryos and meristems, is determined by the "energizing" or "working sphere" of the nucleus, which they considered to be very restricted. Both investigators noted that unusually large or much elongated protoplasts tend to be multinucleate, and Sachs emphasized the fact that large, uninucleated cells either contain much passive (non-cytoplasmic) material or are relatively inactive until energized by the formation of numerous nuclei.

Are Cambial Initials Multinucleate?

The cambium is composed of elements of two distinct shapes and sizes. The ray initials commonly are roughly isodiametric and of the same general order of magnitude as the cells of embryos and terminal meristems. The initials which divide to form the elongated elements of the xylem and phloem, on the contrary, have one long and two short dimensions and are relatively large (figs. 47, 53). In gymnosperms and less highly differentiated dicotyledons, adjacent fusiform initials vary greatly in length and volume. The questions suggest themselves, accordingly: are the ray initials uninucleate and the elongated cells multinucleate, and are the striking variations in the length and volume of the fusiform initials closely correlated with fluctuations in the number of nuclei that are contained within them? Schacht (1856) and Russow (1882) were of the opinion that the elongated cells of the cambium contain more than one nucleus each, but Strasburger (1891) questioned the accuracy of their conclusions.

During the last few years, I have secured material of the cambium from a wide series of gymnosperms and angiosperms of both temperate and tropical regions. The specimens were removed from various parts of the stems, roots, and branches and from trees of different sizes and ages, and, in the case of certain species, were collected at frequent intervals throughout the growing and resting seasons. The tissues were transferred as rapidly as possible to various killing fluids, of which the chrom-acetic-urea solution proved to be the most effective. In none of this material have I found cambial initials which contained more than one nucleus each. As shown in figures 47 and 53, the elongated initials, in tangential, longitudinal sections of the cambium, frequently appear to be multinucleate, but this is due to the fact that several radially flattened cells (fig. 50) are exactly superimposed so that their nuclei lie close to the same focal plane. It is evident, accordingly, that the fusiform cells of the lateral meristem do not resemble other types of large or much elongated protoplasts, such as have been shown, by Schmitz (1879), Treub (1880), Johow (1880), Kallen (1882), Haberlandt (1887), Pirotta and Buscalioni (1898), Smolák (1904), Němec (1910), Lundegårdh (1914), and others, to be multinucleate. Each initial contains a single nucleus which is centrally located and retains this position during growth and karyokinesis. In other words, not only is there a much greater variability in the size of the meristematic cells than hypothesized by Sachs or Strasburger, but in the lateral meristem the nucleus may extend its "energizing" influence to a distance of several thousand microns. Strasburger found that the average diameters of the more or less isodiametric cells of terminal meristems varied between 5 and 24 microns. In certain gymnosperms, the cambial initials may attain a length of more than 9,000 microns and a volume of approximately 10,000,000 cubic microns.

NUCLEO-CYTOPLASMIC RELATION

Strasburger's measurements led him to believe that there is a close correlation between cell size and nuclear size, a conclusion which was strongly supported by the experimental investigations of Gerassimow (1902), and which has led to considerable controversy among zoologists and botanists as to whether the so-called nucleo-cytoplasmic relation is a constant and self-regulating ratio. The painstaking investigations of a number of zoologists indicate that, although in general large cells tend to have larger nuclei than small ones, the nucleo-cytoplasmic ratio fluctuates within rather wide limits, not only in different organisms, but also during different stages in ontogeny and under different environmental conditions. Highly specialized tissue cells tend to have very different ratios from those characteristic of undifferentiated or embryonic elements.

TABLE 1. *Pinus Strobus* L.

	Nucleus				Cell				Ratio Between Volume of Nucleus and Volume of Cell
	Dimensions			Approximate Volume	Dimensions			Approximate Volume	
	VD	RD	TD		VD	RD	TD		
Cambium from 1-year-old stem									
	microns	*microns*	*microns*	*cu. mic.*	*microns*	*microns*	*microns*	*cu. mic.*	
Ray initials	10.8	8.7	6.5	350	22.9	17.8	13.8	5,000	1:14
Large initials	63	3.2	5.8	1,000	870	4.3	16.	60,000	1:60
Cambium from 60-year-old stem									
Ray initials	12.4	12.5	9.9	850	24.8	26.6	17.0	10,000	1:12
Large initials	82	5.9	8.9	3,500	4,000	6.2	42.4	1,000,000	1:286

Basis: dimensions of cells and nuclei are averages of 50 measurements.

The cambial initials of arborescent dicotyledons contain smaller nuclei (figs. 26, 40, 47) than do homologous cells of gymnosperms (figs. 1, 10, 33, 39, 42, 53). Whether this difference is due entirely to the fact that the cambial initials are smaller in the former than in the latter group of plants is a question which must be reserved for discussion in a subsequent paper. In Coniferae, as illustrated by *Pinus Strobus* L., the dimensions and volume of the nuclei vary considerably in cambial initials of different shapes and sizes. The large, fusiform initials have larger and more elongated nuclei than the small, roughly isodiametric, ray initials (figs. 1, 10, 14, and table 1). Furthermore, the large cambial initials of stout, mature stems tend to contain larger nuclei than do the small, meristematic cells of young shoots (table 1). However, as shown in table 2, the nuclei of fusiform initials are subject to variations in their longitudinal dimensions (VD) which are not closely correlated with fluctuations in the length of the cells. The most striking of these variations are seasonal. In the stem of the white pine, the "resting" nuclei of the fusiform initials tend to be much longer and narrower during the fall and winter than during the spring and summer (figs. 1, 10, and table 2). This change, if it occurs, is much less conspicuous in the root (fig. 33). It should be noted, in addition, that the variations in the shape of the nuclei are not paralleled necessarily by similar fluctuations in their volume. This is due to the fact that the changes in length may be more or less completely neutralized by concomitant changes in cross-sectional area.

TABLE 2. *Pinus Strobus* L.

Date	Source of Cambium			Nuclei		Fusiform Initials	
	Age of Tree, Years	Portion of Plant	Number of Rings Under Cambium	Dimensions (Microns)		Dimensions (Microns)	
				VD	TD	VD	TD
3/25/18	36	Stem	1	64	4.5	910	18.6
3/21/18	"	"	8	68	8.1	2090	23.7
3/9/18	"	"	27	67	8.9	2780	29.5
2/25/18	"	Branch	1	60	4.6	830	20.1
2/25/18	"	"	12	60	9.1	1950	27.7
4/22/18	67	Stem	1	56	4.3	800	16.3
3/24/18	"	"	48	82	8.9	3890	42.2
4/28/18	"	"	48	*41*	*17.3*	4000	38.5
3/24/18	"	"	61	84	7.9	3000	32.0
3/23/18	"	Large root	32	42	17.2	2760	40.5
3/2/18	25	Stem	1	56	6.1	890	16.3
3/2/18	"	"	15	57	7.9	2650	39.1
4/22/18*	"	"	19	71	6.3	1700	23.5
4/22/18*	"	"	19	*34*	*13.6*	1700	23.5
5/19/18	"	"	15	*36*	*15.3*	2400	35.3
6/17/18	"	"	17	*39*	*12.8*	3260	35.2
7/15/18	"	"	17	*32*	*16.3*	2970	36.8
8/19/18	"	"	17	*39*	*13.2*	2580	34.4
10/13/18	"	"	19	59	8.3	1710	29.8

Basis: Dimensions of cells and nuclei are averages of 50 measurements.

Italicized figures indicate that the nuclei are from cambial initials which have been dividing for some time previously.

* Both types of "resting" nuclei were present in the same sections, due to the fact that certain initials had divided, whereas others were still in the winter condition.

Although the values in table 1 indicate that the ratio between cell size and nuclear size may remain relatively constant in ray initials of different sizes, they show very clearly that this ratio varies greatly in fusiform initials of different dimensions and volumes. The nuclei do not elongate to any considerable extent as the fusiform initials increase in length. In other words, these meristematic cells do not contain very abnormally elongated nuclei, such as have been described and figured by Molisch (1899) for highly specialized tissue cells of certain monocotyledons. As previously stated, the relatively small, centrally located nucleus must, in certain cases, extend its energizing influence for several thousand microns in order to control processes of growth and longitudinal division in the cambial initials of various gymnosperms.

Boveri (1902, 1905) found that the size of the nuclei in echinoderm larvae is dependent upon the number of chromosomes which enter into the nuclei, and concluded that "die Grösse der Larvenzellen ist eine Funktion der in ihnen enthaltenen Chromatinmenge, und zwar ist das Zellvolumen der Chromosomenzahl direkt proportional." A few years later Gates (1909) showed that *Oenothera gigas*, a tetraploid mutation of *Oe. Lamarckiana*, is composed of larger cells than the species from which it originated. Similar phenomena have been observed by Gregory (1912), Winkler (1916), and others. The work of Gregory (1909) and Keeble (1912) indicates, however, that in certain giant forms of *Primula sinensis*, which have larger cells than the typical form, there is an increase in the size, but not in the number of chromosomes. Winkler's paper is particularly significant, in this connection, owing to his general discussion of the relation between cell size and chromosomal number in the higher plants. He reaches the conclusion that there is a very close correlation between cell size and chromosomal mass, both in meristematic and non-meristematic, somatic tissue. He states that in embryonic types of tissue (lateral and terminal meristems) the cells are roughly isodiametric, of nearly uniform size, and always contain the diploid number of chromosomes. In non-meristematic tissue, multinucleate protoplasts, nuclear fusions, and changes from the diploid to the tetraploid or the polyploid condition are of common occurrence, and many cells depart widely from the inherited, specific cell size of the plant. He infers that such cells tend to be hyperchromatic, much elongated elements containing more than one nucleus each and other types of large cells an abnormal number of chromosomes.

It is evident that the cambium provides a favorable medium for testing Winkler's generalizations. The fusiform initials, *which vary greatly in size*, obviously are not multinucleate. Are they hyperchromatic? Before attempting to answer this question it is essential to devote some attention to a discussion of karyokinesis in the lateral meristem.

KARYOKINESIS IN CAMBIAL INITIALS

As far as I have been able to determine, the nuclei of cambial initials always divide mitotically. Strasburger (1891) observed fragmentation in young sieve tubes of larch. My own preparations indicate that amitosis may occur in slightly differentiated cells of the cambial layer—which later are to develop into tracheary elements—just before the beginning of the growing season (fig. 38). Vacuolated nuclei also tend to be present at this time (fig. 38).[1] However, I have never seen any indication of either of these phenomena in undoubted *initials* of the lateral meristem of either gymnosperms or dicotyledons.

The cambium varies so greatly in its activities during different seasons, in different plants, and in different parts of given individuals, that the only rules which I have been able to formulate for obtaining division figures are, to collect specimens at frequent intervals, from as many individuals as possible, and from all parts of each plant. Initials may be dividing actively in one portion of a stem when those in adjacent portions are inactive. Similarly, numerous mitotic figures may be present in a given individual when a neighboring plant appears to be entirely devoid of them.

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[1] I am not entirely convinced that the phenomena observed by Strasburger and myself are not artifacts produced by poor fixation.

The karyokinetic figures in ray initials (figs. 15, 16, 30, 31, 32) generally resemble those that occur in parenchyma and terminal meristems. The figures vary considerably in fusiform initials, depending upon the shape and size of the nuclei and cells, and upon the plane in which the cells are dividing. Of course, the principal plane of division in elongated initials is periclinal or parallel to tangents to the circumference of the stem or root. In other words, the fusiform initials divide in a tangential, longitudinal plane which is a division plane of maximal area. Although the tangential diameter of the cambial initials increases to a certain extent during the earlier stages of enlargement of stems, roots, and branches (table 1), it falls far short of being sufficient to compensate for the rapid increase in the periphery of the cambium. Nägeli (1864) inferred from this fact that the fusiform initials must divide periodically in a radial, longitudinal plane. These hypothetical radial, longitudinal divisions are described and figured in many botanical textbooks, but I have been unable to find them in any of the gymnosperms and less highly specialized dicotyledons that I have studied. As shown by Robert Hartig (1895) and Klinken (1914)—for *Pinus sylvestris* L. and *Taxus baccata* L.—the fusiform initials elongate, sliding by one another, until they have attained a certain length. They then divide, by means of a more or less oblique, transverse partition into two short cells, which in turn elongate and divide. Thus, the increase in the periphery of the cambium is due primarily, not to radial, longitudinal divisions of the fusiform initials, accompanied by lateral enlargements of the products of such divisions, but to the sliding growth of periodically elongating and dividing cells. During the process of elongation, between successive pseudo-transverse divisions, the initials continue to divide in a tangential, longitudinal plane.

In dicotyledons (*e.g.*, Robinia) having short initials and small nuclei, the polar axis of the karyokinetic figure in a longitudinally dividing cell is placed at right angles to the main axis of the cell (fig. 25). In *Pinus Strobus* and other gymnosperms, on the contrary, it tends to assume a diagonal position during the late prophase, metaphase, anaphase, and early telophase (figs. 4, 5, 17, 18, 19). That this is not an artifact, due to the displacement of an ordinary spindle during fixation or sectioning, is indicated by the fact that the whole mitotic figure is asymmetrically developed in conformity with its oblique position (figs. 17, 18, 19). Furthermore, it should be noted that the radial diameter of the initials is so short (fig. 50) that there is not sufficient room to permit the elongated nucleus to shift into, or the karyokinetic figure to develop in, a transverse position. Of course, the position of the mitotic figure in pseudo-transversely dividing fusiform initials (figs. 7, 8, 9, 11, 12, 13, 28, 29) cannot be due to such factors as these, but is closely correlated with the orientation of the division membrane. When the partition is exactly transverse, the polar axis of the karyokinetic figure is parallel to the long axis of the cell (figs. 7, 9, 28, 29), but when it is oblique the division figure tends to assume a diagonal position (figs. 8, 11, 12, 13). In ray initials and in longitudinally dividing fusiform initials of *Pinus Strobus*, the chromosomes tend to be twisted and crowded together in the nuclear plate (figs. 4, 15), but in wide,[2] pseudotransversely dividing fusiform initials, the nuclear plate may be more extensive and the chromosomes so arranged that they are nearly all visible in a single focal plane (figs. 8, 12). Furthermore, the chromosomes in adjoining cells may vary considerably in shape, in certain figures resembling hooks (fig. 12), and in others V's or U's of varying widths (figs. 7, 8, 15). The shape of the karyokinetic figures, particularly during the prophase, is profoundly affected by the shape of the "resting" nuclei. Thus, the spirems formed in the stem at the beginning of the growing season, when the nuclei are much elongated (figs. 10, 11, 41), may be entirely unlike those which are formed subsequently from shorter and wider nuclei (figs. 1, 6).

NUCLEO-CYTOPLASMIC RELATION (*continued*)

In order to determine whether large meristematic cells are hyperchromatic, I have devoted considerable attention to a study of the number and size of the chromosomes in the cambium of *Pinus Strobus* L. Sections were secured showing adjacent meristematic cells of various dimensions and volumes in equivalent stages of karyokinesis. The large, fusiform initials do not contain the tetraploid or polyploid number of chromosomes. All cells regardless of their size have approximately the diploid number (24).[3] It is evident, accordingly, that the variations in the size of the nuclei and cambial initials of *P. Strobus* are not dependent upon variations in the number of chromosomes. Are they correlated with fluctuations in the size of chromosomes?

Erdmann (1908) concluded from her investigations upon sea urchins that chromosomal mass, rather than chromosonal number, is the size-determining factor of cells. Conklin (1912) considered that in comparable cells of Crepidula large protoplasts have larger nuclei and chromosomes than small protoplasts. Hegner (1920) reaches similar conclusions in a recent paper upon Arcella. If there is a close correlation between chromosomal mass and volume of cytoplasm, the adjacent cells of the cambium vary so greatly in volume that there should be a striking contrast in the size of their chromosomes. This does not appear to be the case, however, in any of the material that I have studied. The chromosomes in a small ray initial having a capacity of 3,000–10,000 cubic microns may be fully as long and thick as those which occur in an adjoining fusiform initial with a volume of 1,000,000–5,000,000 cubic microns. Figures 4, 5, 17, 18, 12, 13, 28, and 29 are from fusiform initials having capacities of 800,000–1,200,000 cubic microns, and figures 15, 16, 30, and 31 from ray initials with volumes of 5,000–10,000 cubic microns. The chromosomes in figure 12 appear to be longer than those in figures 4 and 15 because they are flat, hook-shaped, and visible in one focal plane, whereas those in the other figures are U-shaped, twisted, and in different focal planes. Of course, as admitted by Conklin, it is difficult to determine the volume of individual chromosomes with any considerable degree of accuracy, but comparisons between figures 4, 7, and 15; 5, 13, and 16; 17, 28, and 30; and 18, 29, and 31 indicate very clearly that the large, fusiform initials of the lateral meristem are not hyperchromatic. The striking variations in the size of the nuclei (figs. 10 and 14) are due to differences in the volume of their achromatic portions. Thus, the volume of nucleolar matter is much greater in the large nuclei. Furthermore, the staining reactions of the "resting" nuclei suggest that the chromatin is more concentrated in the smaller than in the larger nuclei. In chromatin stains, the small nuclei of ray initials are very heavily overstained long before the large nuclei of adjoining fusiform initials become clearly differentiated.

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[2] Tangential dimension.

[3] Miss Ferguson (1904) has shown that the haploid number is 12.

It is evident, accordingly, that, although in certain cases variations in the volumes of cells are closely associated with fluctuations in the number of chromosomes (Boveri, Gates, Winkler) and in others with fluctuations in the size of chromosomes (Erdmann, Gregory, Keeble, Conklin, Hegner), the undifferentiated, actively dividing cells of the lateral meristem may vary greatly in size without corresponding variations in chromosomal size or number.

CYTOKINESIS

Certain of the fusiform initials in Coniferae are several hundred times as long as they are wide (radially), yet they divide longitudinally. What then is the nature of cytokinesis in cells of such extraordinary dimensions? During the telophase (fig. 17) the central spindle expands laterally by the addition of peripheral fibers and gradually assumes the form of a more or less warped disk (fig. 18). The connecting fibers, and later the accessory fibers, thicken to produce a cell plate in the usual manner, and then the fibers disappear except for a circular rim of kinoplasm. In tangential, longitudinal sections of the cambium, this ring-shaped aggregation of kinoplasmic fibrillae forms a halo about the daughter nuclei (fig. 56).[4] The ring increases in circumference by the addition of new peripheral fibers and extends the cell plate as it does so. When it intersects the radial walls of the cell, it becomes more or less four-sided (fig. 57). As soon as the cell plate comes in contact with the radial facets of the protoplast, the kinoplasm disappears from two sides of the frame-like figure, leaving two entirely separate aggregations of kinoplasmic fibrillae, which are parallel and which cross the cell from one radial wall to the other (fig. 58). These rod-like masses of kinoplasm (kinoplasmasomes) move in opposite directions, thereby extending the cell plate towards the ends of the cell. In radial, longitudinal sections of the cambium, the kinoplasmasomes are seen in section (figs. 20, 21). They are located midway between the tangential facets of the cell and usually are equidistant from the daughter nuclei or approximate center of the protoplast. This indicates, of course, that they move forward at equal rates. As shown in figure 22, they have a wedge-shaped outline, bluntly convex in front and tapering to a point at the rear along the cell plate. They are composed of fibrillae which resemble those that occur in the spindle. The threads or "lines of flow" do not extend across the cell from one tangential membrane to the other, but lie free in the cytoplasm. Nor are they connected with the daughter nuclei, which remain in their original position near the center of the protoplast. As new peripheral fibers are successively added in front, those at the rear disappear from about the recently formed portion of the cell plate (fig. 22). The latter is gradually extended in this singular fashion, often for a distance of several thousand microns, until it eventually reaches the ends of the protoplast; thus dividing the latter into halves, each of which contains one of the daughter nuclei. The nuclei become enclosed in a nuclear membrane and reform their nucleoli long before the kinoplasmasomes reach the ends of the cell.

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[4] Beer and Arber (1915) reached the conclusion that binucleate cells are of common occurrence in the growing tissues of the higher plants. They state: "The nuclei of the multinucleate cells generally arise by mitosis, but there are certain exceptional features connected with this mitosis and with the behavior of the associated protoplasm. The most striking of these is that two daughter-nuclei in the telophase, between which no wall-formation is in progress, are often found enclosed in a hollow sphere of dense and deeply staining protoplasm, the appearance at first glance suggesting a cell within a cell." I strongly suspect that the phenomenon referred to by them is a phase of cytokinesis not unlike that illustrated in figure 56.

Similar phenomena occur in dicotyledons during longitudinal division of the fusiform initials (figs. 23, 24, 25), but, owing to the smaller size of the cells, the kinoplasmasomes and cell plates are smaller than in the Coniferae. The oblique partitions of fusiform initials, and the longitudinal and oblique divisions of their derivative cells, are also formed by the intervention of these extraordinary cell plates (figs. 27, 51, 54, 55). Furthermore, the writer has accumulated considerable evidence which indicates that the phenomena in question are not confined to the cambial layer, but that they occur in other somatic tissues of the higher plants, in elongated or much flattened cells whose planes of division have one long and one short dimension.

Types of Cell Plate Formation in the Higher Plants

It is of interest to inquire what relation this type of cell plate formation —which is so greatly extended, both as regards space and time, and so clearly dissociated, except in its initial stages, from the usual phenomena of karyokinesis—bears to those types which previously have been described by Treub (1878), Strasburger (1880), and Schürhoff (1906). In Treub's first type, the nucleus is centrally located and the central spindle merely expands symmetrically until it touches the four walls of the isodiametric cell. In his second type, the nucleus lies near one wall and the daughter nuclei and "fibrillar-complex" migrate to the opposite side during cytokinesis. Strasburger described a third type, in which the daughter nuclei remain on one side of the cell and the "fibrillar-complex" crosses it. Schürhoff found a fourth type, in large cells having centrally located nuclei and small spindles. It differs from the preceding types in that "mit der Neubildung der peripheren Cytoplasmafäden geht die Auflösung der zentralen Strahlungen Hand in Hand."[5] In other words, a ring or halo of kinoplasm is formed such as occurs in cambial initials during incipient stages of cytokinesis.

A comparative study of cell plate formation in different somatic tissues, and in cells of different shapes and sizes, suggests that the various types of phenomena, described by Treub, Strasburger, Schürhoff, and the writer, are but different phases or stages of a single general or fundamental type of cytokinesis. The particular expressions of the phenomenon which may occur in any given cell are dependent upon its dimensions, its plane of division, and the size and location of the nucleus. Thus, in very small, isodiametric cells having a large, centrally located nucleus, the cell plate quickly intersects the walls of the cell without any extensive lateral enlargement of the central spindle. In larger cells with small nuclei, there is sufficient room for the process of cytokinesis to reach the halo or frame stage before the cell plate intersects the sides of the cell. However, only in elongated or much flattened elements is it possible for the phenomenon of cell plate formation to pass through the spindle, disk, halo, and frame stages, and finally to form two entirely separate aggregations of kinoplasmic fibrillae, kinoplasmasomes.

All five types of cytokinesis may be found in the cambium. Treub's first type occurs in ray initials (fig. 31) and in transversely dividing fusiform initials (figs. 29, 49). Schürhoff's type also is present in certain ray initials (fig. 32) and transversely dividing fusiform initials (fig. 48). Although the nuclei are centrally located under normal conditions, I have found them in a lateral position in Sequoia, in fusiform initials which were dividing to form callus. During cytokinesis the daughter nuclei remained on one side of the cell, as in Strasburger's preparations (figs. 45, 46), or one or both of them migrated across the cell, as in Treub's second type of cytokinesis (fig. 52).

SIGNIFICANCE OF CYTOKINESIS IN THE CAMBIUM

The formation of the cell plate in cambial initials promises to be significant in the discussion of a number of fundamental cytological and physiological problems.

Strasburger's (1875, 1880, 1882) suggestion that spindle fibers are of cytoplasmic origin and his conclusion that the cell plate originates in swellings of the connecting spindle fibers have been questioned by various investigators. Treub (1878) held that the cell plate arises from free cytoplasmic granules which migrate into the equatorial region of the spindle, and Zacharias (1888) contended that the spindle is of nuclear, and the cell plate of cytoplasmic, rather than of kinoplasmic, origin. Mottier (1900) found that in certain of the higher plants the connecting fibers do not thicken appreciably in the equatorial region, and do not lie sufficiently close together to enable the slightly thickened middle parts to meet and fuse. He concluded from this "that the cell plate is formed by a homogeneous plasma which is conveyed to the cell plate region and deposited there by the connecting fibers." Strasbürger's generalization concerning the kinoplasmic origin of the cell plate was ably defended by Timberlake (1900), who concluded, however, that the nucleus "is the center of metabolic processes concerned in the production of the kinoplasm."

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[5] A phenomenon previously noted by Went (1887).

Strasburger (1880) and Went (1887) noted that the connecting spindle fibers appear to increase in number prior to the formation of the cell plate, and the former investigator subsequently suggested that this increase might be due to a splitting of the original fibrillae. Timberlake endeavored to prove that the lateral expansion of the spindle is not due to the formation of new fibers, but to the separation and enlargement of the original connecting fibers, coupled in certain cases with the addition of peripheral threads, formed from fibers which radiate from the daughter nuclei.

Hof (1898) and Němec (1899) showed that after the cell plate is complete the connecting fibers appear to be "drawn in" toward the cell plate and their place taken by granular cytoplasm. Timberlake stated that "concurrent with the growth of the cell plate in extent and the disappearance of the fibers from a central portion of the spindle the nuclei come to lie nearer the cell plate." He concluded that "all of the fibers which form cell plate elements are completely used up in the growth of the cell plate," and that "during the period of growth the cell plate may so shift its position as to lie in a plane different from that in which it was first formed."

The formation of the cell plate in cambial initials is significant in these connections. There is an enormous increase in the number of "peripheral" fibers during cytokinesis. As in the case of the radial fibrillar systems, which Harper and Dodge (1914) have shown to function in the formation of the capillitium of certain Myxomycetes, the kinoplasmic fibers have no visible connection with the nuclei. They are so far removed from the nuclei (figs. 20, 21) during the later stages of cytokinesis that one is inclined to question Timberlake's generalization concerning the nuclear origin of kinoplasm. The phenomena appear rather to justify Strasburger's contention that the accessory fibers are of cytoplasmic origin. As the original connecting fibers "draw in" or disappear, the nuclei tend to move towards the cell plate (figs. 19, 32, 45, 55), but subsequently may move away from it (figs. 21, 27). That the connecting fibers may thicken considerably in the equatorial region of the spindle is shown in figure 30; but a discussion of the finer details of cell plate formation is reserved for a subsequent paper. The width of the kinoplasmasomes closely approximates that of the central spindle. In other words, broad kinoplasmasomes tend to occur in cells having large karyokinetic figures (figs. 27, 29) and narrower ones in elements having smaller spindles (figs. 17, 18, 19, and 20; figs. 25, 24, and 23, and figs. 31 and 32).

The phragmoplasts develop along straight lines or curves depending upon the orientation of the karyokinetic figure and the plane in which the initial is dividing. In longitudinally dividing fusiform initials, in which the polar axis of the karyokinetic figure is transverse (fig. 25), the kinoplasmasomes move toward the ends of the protoplast along its longitudinal axis (figs. 23 and 24). When the mitotic figure occupies a diagonal position (fig. 17), the phragmoplast, during its earlier stages, curves toward the center of the protoplast avoiding the tangential facets of the cell (figs. 18, 19), and subsequently straightens out as shown in figures 20 and 21. In obliquely dividing cells having diagonally oriented division figures, either the phragmoplast develops in a single plane (figs. 27, 51, and 52), or the kinoplasmasomes meander more or less, forming undulating or curved partitions (fig. 54). In the formation of new ray initials, which are carved out of fusiform initials, both kinoplasmasomes may, in certain cases, curve toward and intersect the same radial surface of the cell.

Thompson (1917) is of the opinion that Errera's (Plateau's) law of minimal area is not invalidated by the occurrence of oblique or curved partitions provided these membranes are sigmoid and intersect the older walls at right angles. De Wildeman (1893) found that in certain cells the polar axis of the division figure shifts to a diagonal position previous to the formation of the cell plate, which curves during its development so as to intersect the sides of the cell at right angles. That all diagonal partitions do not develop in this manner is indicated very clearly by the phenomena in the cambium. The writer (1920*a*) has shown that the kinoplasmasomes, cell plates, and young membranes intersect the sides of the cell at varying degrees of acuteness, as well as at right angles. This suggests, of course, that in dealing with cytokinesis we are not concerned with protoplasm in liquid or semi-liquid phases. In other words, cellular membranes, at the moment of their formation, frequently do not assume the forms which would be assumed, under similar conditions, by liquid films destitute of weight (Plateau).

NUCLEOLI

The cambium of Coniferae appears to be an unusually favorable medium for the study of the structure and function of nucleoli, which are unusually large and conspicuous in most representatives of the family (Pls. XXVI, XXVII). In *Pinus Strobus* they vary greatly in size, shape, and number in different initials (figs. 1, 10, 14, 33). They are clearly visible during the early prophases (figs. 6, 41) and late telophases. Many of my preparations suggest that the large nucleoli are composed of aggregations of smaller nucleolar masses (fig. 43). During the process of aggregation hollow spheres (fig. 44) may be formed which resemble "vacuolated" nucleoli. The larger nucleoli also appear to fuse in many cases (figs. 1, 33, 41), particularly in cells which are differentiating into tracheary elements or sieve tubes (fig. 35*a*).

If nucleoli actually are concerned in the growth or enlargement of chromosomes, as is maintained by various botanists, one might expect the nuclei of fusiform initials (fig. 10), which contain a relatively large volume of nucleolar matter, to form much larger chromosomes than the small nuclei of ray initials (fig. 14). This is not the case, however, in *Pinus Strobus*, as I have shown on preceding pages.

There is a striking contrast between the cambial nucleoli of gymnosperms and those of dicotyledons. The latter tend to be surrounded by a conspicuous halo (fig. 40), which is absent in the Coniferae (Pls. XXVI, XXVII). Of course, this halo is supposed to be an artifact (Nägeli), yet the fact that it occurs so constantly in one group and not in the other suggests that it may be significant from the morphological or the physicochemical point of view.

Schwarz (1884) and Zacharias (1895) noted that during the differentiation of tissue elements in the growing points of plants, the volume of the nucleoli, as of the nuclei, first increases and then decreases. Similar phenomena occur in the cambial zone of *Pinus Strobus*. During the early stages of the differentiation of tracheids and sieve tubes, the nuclei become coarsely granular. The nucleolar mass subsequently decreases (figs. 35, 36, 37), and the nucleus becomes profoundly modified in shape and loses its staining capacity (figs. 36, 37). As suggested by Strumpf (1898), the crumpling of the nucleus (fig. 37) in young sieve tubes may be mistaken for fragmentation.

In conclusion, it is to be emphasized that this paper merely presents the results of a reconnaissance of cytological phenomena in the cambium. Its primary object is to outline salient features of the more striking phenomena encountered, and to pave the way for subsequent and more detailed investigations, on the part both of the writer and of others who may become interested in the cambium as an unusually favorable medium for the study of certain cytological and physiological problems.

I am indebted to my friends, Doctors C. E. Allen, R. A. Harper, W. J. V. Osterhout, and C. E. McClung for a number of helpful suggestions.

Summary and Conclusions

1. The initials of the lateral meristem or cambium, which may attain a length of more than 9,000 microns and a capacity exceeding 10,000,000 cubic microns, are uninucleate. The working sphere of their nuclei must extend in certain cases for a distance of several thousand microns.

2. The nucleo-cytoplasmic ratio may be relatively constant in ray initials, but varies enormously in fusiform initials.
3. All of the cambial initials of *Pinus Strobus*, regardless of variations in size, contain the diploid number of chromosomes.
4. Small ray initials having a capacity of 5,000–10,000 cubic microns may contain as large chromosomes as adjacent fusiform initials with a volume of 1,000,000–5,000,000 cubic microns.
5. Fusiform initials, which frequently are several hundred times as long as they are wide, divide longitudinally by an extraordinary extension of the cell plate.
6. The various types of cell plate formation that have been described by Treub, Strasburger, Schürhoff, and the writer appear to be merely different phases or stages of a single general type of cytokinesis.
7. The significance of the cambium in the investigation of various cytological problems, particularly of those relating to the cell plate and the dynamics of cytokinesis, is briefly discussed.

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DESCRIPTION OF PLATES

PLATE XXVI

FIG. 1. *Pinus Strobus* L. "Resting" nucleus from fusiform initial, showing characteristic shape during spring–summer. Tangential, longitudinal extension. × 850.

FIG. 2. Same. Nucleus from longitudinally dividing, fusiform initial, seen in radial, longitudinal extension. Early prophase. × 850.

FIG. 3. Same.. Later prophase. × 850.

FIG. 4. Same. Oblique position of karyokinetic figure, metaphase. × 850.

FIG. 5. Same. Early anaphase. × 850.

FIG. 6. Same. Karyokinetic figure from transversely dividing, fusiform initial, seen in tangential, longitudinal extension. Spirem formed by short, wide type of resting nucleus. × 850.

FIG. 7. Same. Metaphase from transversely dividing, fusiform initial, seen in tangential, longitudinal extension. × 850.

FIG. 8. Same. Metaphase from wide, obliquely dividing, fusiform initial, seen in tangential, longitudinal extension. × 850.

FIG. 9. Same. Late anaphase from narrow, transversely dividing, fusiform initial, seen in tangential, longitudinal extension. × 850.

FIG. 10. Same. "Resting" nucleus from fusiform initial, showing characteristic elongated, fall–winter shape. Tangential, longitudinal extension. Compare figure 1. × 850.

FIG. 11. Same. Elongated type of spirem formed by elongated nucleus. Compare figure 6. × 850.

FIG. 12. Same. Metaphase from obliquely dividing fusiform initial, seen in tangential, longitudinal extension. × 850.

FIG. 13. Same. Anaphase from obliquely dividing fusiform initial, seen in tangential, longitudinal extension. × 850.

FIG. 14. Same. "Resting" nucleus in ray initial. × 850.

FIG. 15. Same. Metaphase in ray initial. × 850.

FIG. 16. Same. Anaphase in ray initial. × 850.

PLATE XXVII

FIG. 17. *Pinus Strobus.* Early telophase from longitudinally dividing fusiform initial, seen in radial, longitudinal extension. × 850.

FIG. 18. Same. Widening of central spindle and beginning of cell plate formation. Longitudinally dividing fusiform initial, seen in radial, longitudinal extension. × 850.

FIG. 19. Same. Later stage than that shown in figure 18, showing disappearance of connecting fibers and movement of nuclei toward the cell plate. × 850.

FIG. 20. Same. Later stage than that shown in figure 19, showing daughter nuclei, cell plate, and kinoplasmasomes. × 850.

FIG. 21. Same. Later stage than that shown in figure 20, showing movement of kinoplasmasomes in opposite directions toward ends of protoplast and daughter nuclei in original positions at center of cell. × 400.

FIG. 22. Same. Section of kinoplasmasome showing fibrillæ and cell plate. × 2000.

FIG. 23. *Robinia Pseudo-Acacia* L. Fusiform initial in radial, longitudinal extension, showing cell plate, kinoplasmasomes, and daughter nuclei. × 850.

FIG. 24. Same. Less advanced stage of cytokinesis. × 850.

FIG. 25. Same. Beginning of cell plate formation. Note transverse position of polar axis of division figure. × 850.

FIG. 26. Same. "Resting" nucleus of fusiform initial, seen in radial, longitudinal extension. × 850.

FIG. 27. *Pinus Strobus.* Cytokinesis in obliquely dividing fusiform initial, seen in tangential, longitudinal extension. One daughter nucleus out of plane of section. × 850.

FIG. 28. Same. Early telophase in transversely dividing fusiform initial, seen in tangential, longitudinal extension. × 850.

FIG. 29. Same. Later phase than that of figure 28, showing extension of spindle and beginning of cell plate formation. × 850.

FIG. 30. Same. Thickening of connecting fibers in equatorial region of spindle. Ray initial. × 850.

FIG. 31. Same. Later stage than that shown in figure 30, showing cell plate. × 850.

FIG. 32. Same. Later stage than that of figure 31, showing extension of cell plate and "drawing in" of fibers and nuclei. × 850.

Figures 2, 3, 4, 5, 17, 18, 19, 20, and 21 of Plates XXVI and XXVII illustrate successive stages of karyokinesis and cytokinesis in a longitudinally dividing fusiform initial of a conifer (radial, longitudinal extension). Figures 15, 16, 30, 31, and 32 illustrate a similar series for a ray initial, and figures 26, 25, 24, and 23, a series for a short fusiform initial of a highly specialized type of dicotyledon.

PLATE XXVIII

FIG. 33. *Pinus Strobus.* "Resting" nucleus from fusiform initial of root, showing shape during winter. Contrast figure 10. × 850.

FIG. 34. Same. Nucleus from fusiform derivative cell which is in the earliest stages of differentiation into tracheary element. × 850.

FIG. 35. Same. Later stage than that of figure 34. × 850.

FIG. 35*a*. Same. Fusion of large nucleoli. × 850.

FIG. 36. Same. Later stage than that shown in figure 35. × 850.

FIG. 37. Same. Nucleus from young, differentiating sieve tube. × 850.

FIG. 38. Same. Fragmentation of nucleus and nuclear vacuoles in derivative cells of cambium. × 450.

FIG. 39. *Juniperus virginiana* L. Nucleus from fusiform initial seen in tangential, longitudinal extension. × 850.

FIG. 40. *Sassafras officinale* Nees et Eberm. Nucleus from fusiform initial, showing halos about nucleoli. Tangential, longitudinal extension. × 850.

FIG. 41. *Pinus Strobus.* Nucleus from fusiform initial, showing early prophase and nucleoli. Tangential, longitudinal extension. × 850.

FIG. 42. *Cedrus libani* Barrel. Nucleus from fusiform initial, showing nucleoli. Tangential, longitudinal extension. × 850.

FIG. 43. *Pinus Strobus.* Aggregating nucleolar masses. × 2000.

FIG. 44. Same. Vacuolated nucleoli. × 2000.

PLATE XXIX

FIG. 45. *Sequoia sempervirens* Endl. Cytokinesis in fusiform initial which is dividing to form callus. × 850.

FIG. 46. Same. Later stage than that of figure 45. × 850.

FIG. 47. *Robinia Pseudo-Acacia.* Tangential, longitudinal section of cambium, showing ray and fusiform initials. × 110.

FIG. 48. *Pinus Strobus.* Cytokinesis in transversely dividing, fusiform initial. Tangential, longitudinal extension. × 850.

FIG. 49. *Sequoia sempervirens.* Cytokinesis in transversely dividing fusiform initial. Tangential, longitudinal extension. × 850.

FIG. 50. *Pinus Strobus.* Transverse section of cambium and adjoining xylem and phloem. × 110.

FIG. 51. *Sequoia sempervirens.* Cytokinesis in obliquely dividing fusiform initial. Tangential, longitudinal extension. × 500.

FIG. 52. Same. Cytokinesis; daughter nuclei have migrated to opposite sides of cell. × 500.

FIG. 53. *Pinus Strobus.* Tangential, longitudinal section of cambium, showing two types of initials. × 110.

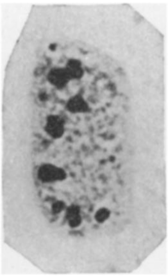
FIG. 54. Same. Cytokinesis in derivative cell of cambium, showing curvature of cell plate. × 500.

FIG. 55. Same. Cytokinesis in obliquely dividing fusiform initial, seen in tangential, longitudinal extension. × 500.

FIG. 56. Same. Halo or "cell within cell" stage of cytokinesis in longitudinally dividing fusiform initial, seen in tangential, longitudinal extension. × 500.

FIG. 57. Same. Later stage than that shown in figure 56. × 500.

FIG. 58. Same. Later stage than that of figure 57, showing kinoplasmasomes. × 500.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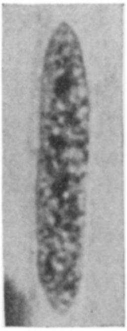
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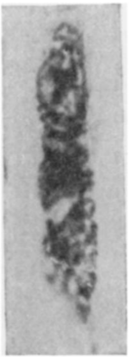
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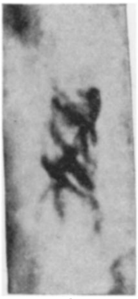
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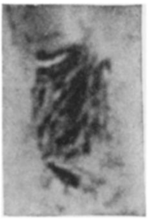
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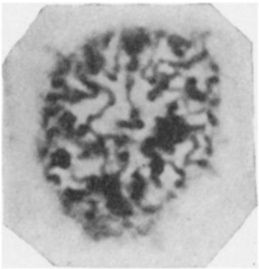
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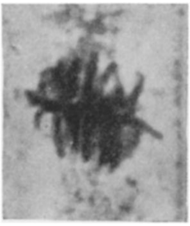
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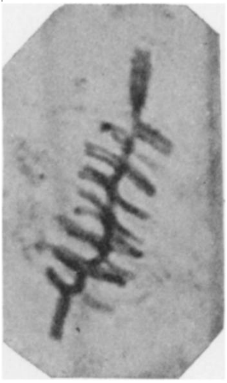
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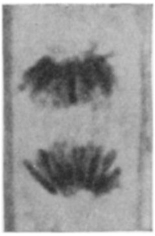
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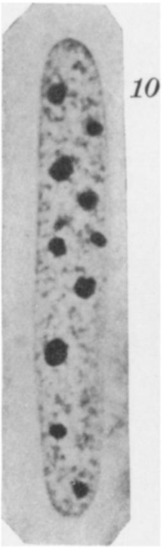
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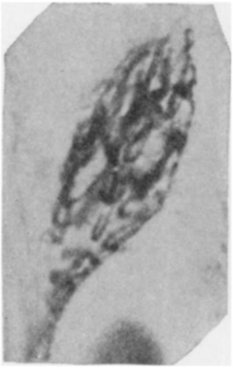
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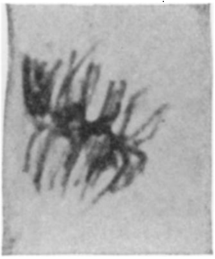
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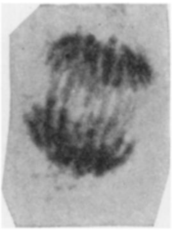
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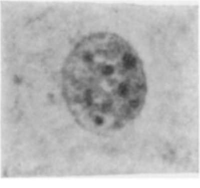
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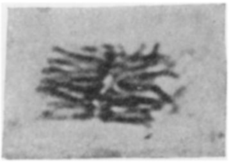
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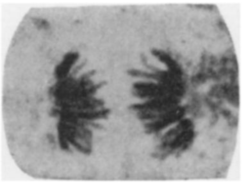
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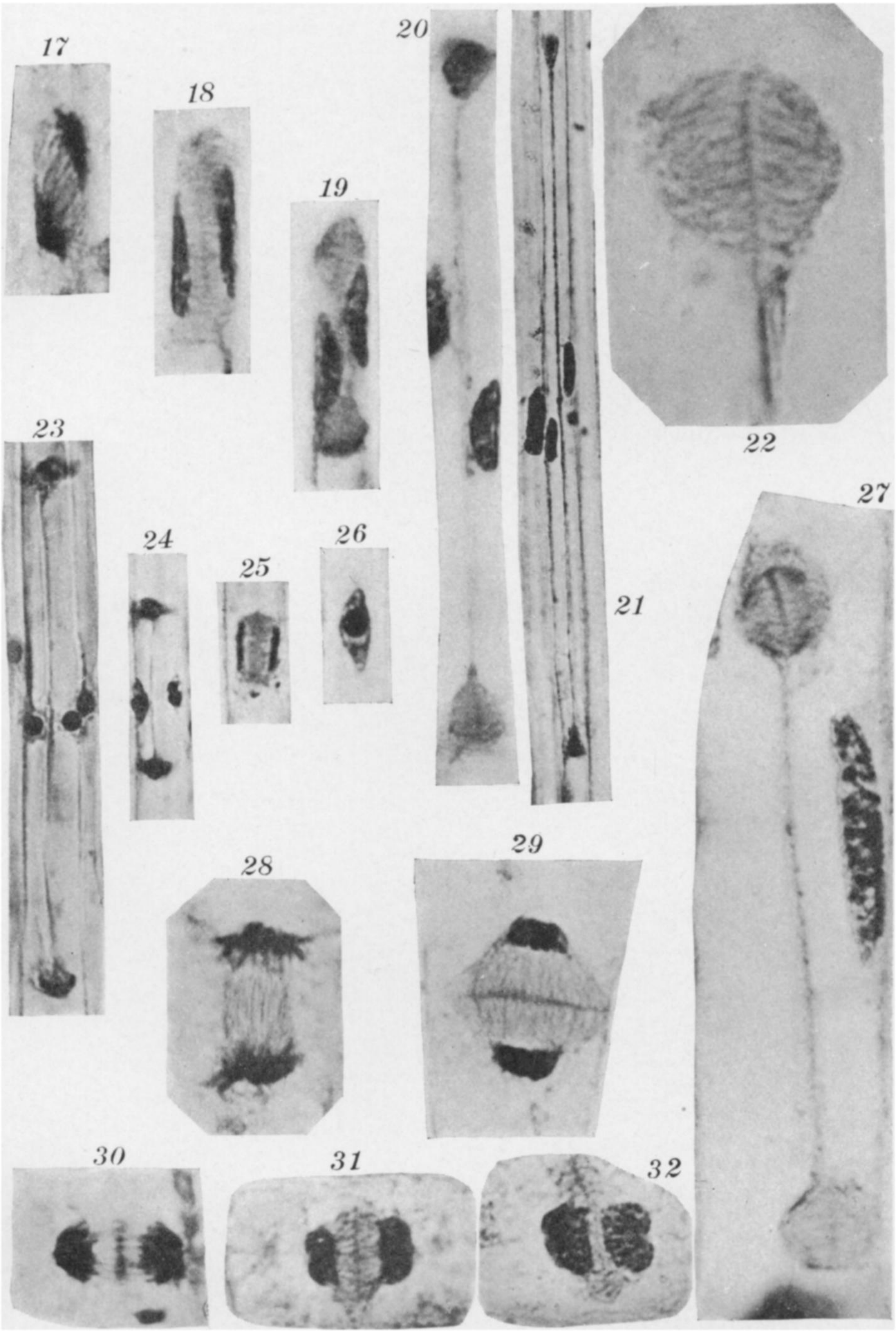
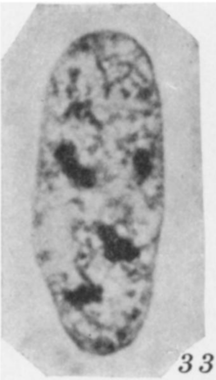
BAILEY: CYTOLOGICAL PHENOMENA IN CAMBIUM.



BAILEY: CYTOLOGICAL PHENOMENA IN CAMBIUM.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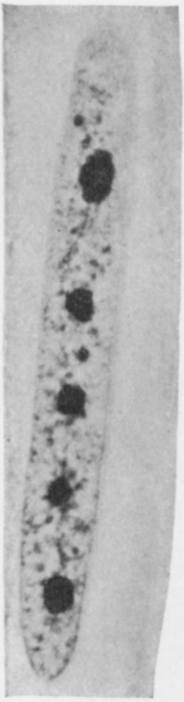
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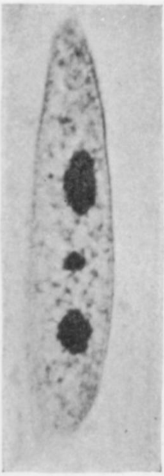
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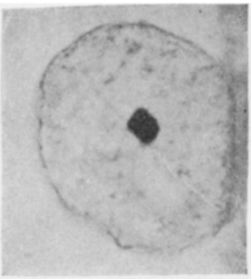
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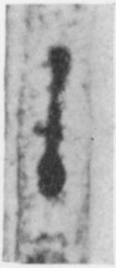
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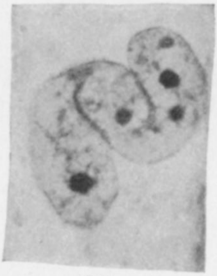
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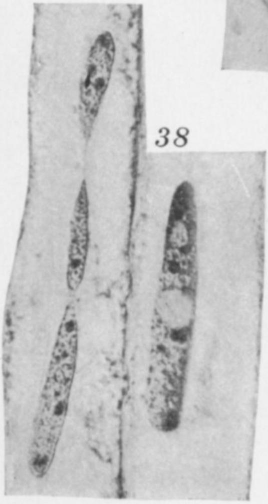
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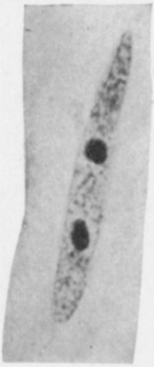
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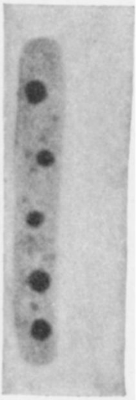
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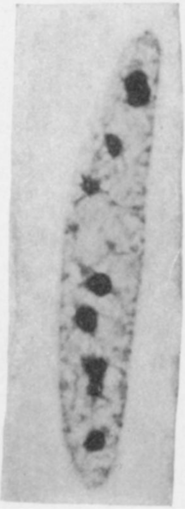
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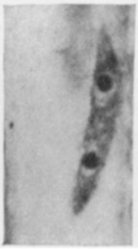
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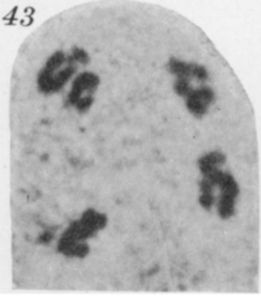
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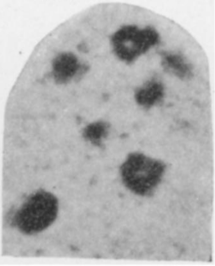
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BAILEY: CYTOLOGICAL PHENOMENA IN CAMBIUM.

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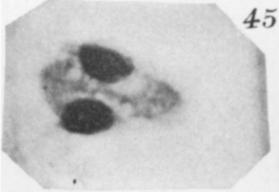

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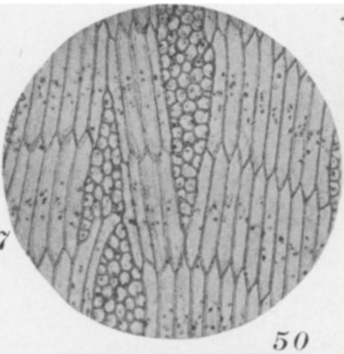

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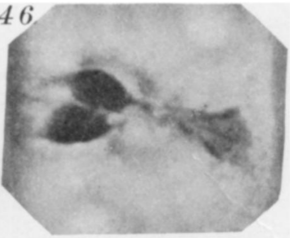

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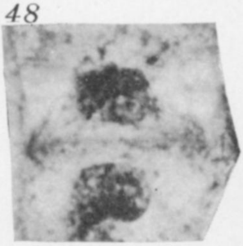

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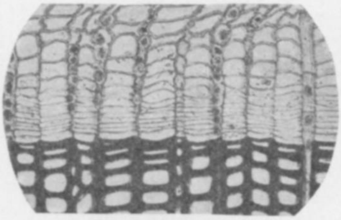

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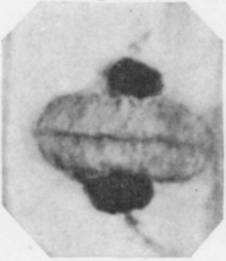

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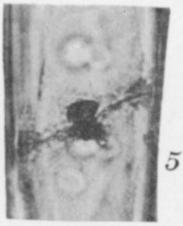

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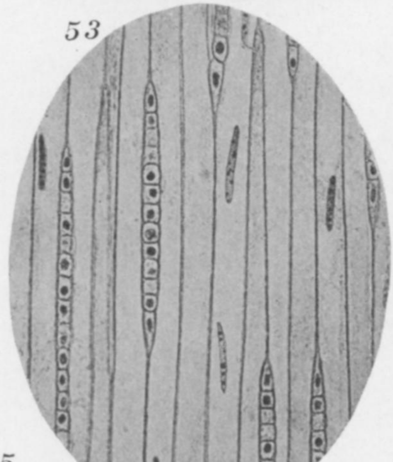

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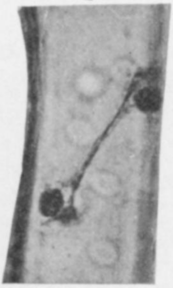

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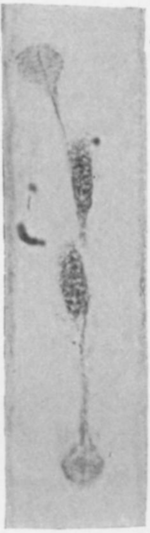

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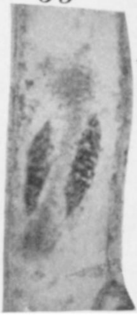

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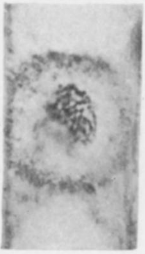

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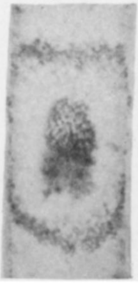

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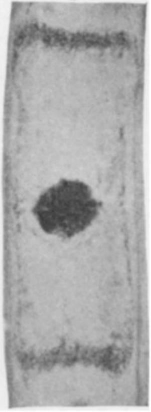

Bailey: Cytological phemomena in cambium.